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High Photosynthetic Capacity in a Shade-Tolerant Crassulacean Acid Metabolism Plant[1]

Implications for Sunfleck Use, Nonphotochemical Energy Dissipation, and Susceptibility to Photoinhibition

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Aechmea magdalenae **André ex Baker, a constitutive Crassulacean acid metabolism (CAM) plant from the shaded Panamanian rain forest understory, has a maximum photosynthesis rate 2 to 3 times that of co-occurring C_3 species and a limited potential for photosynthetic acclimation to high light. Chlorophyll fluorescence measurements indicated that (a) compared with co-occurring C_3 species, photosynthetic electron transport in *A. magdalenae* responded more rapidly to light flecks of moderate intensity, attained a higher steady-state rate, and maintained a lower reduction state of plastoquinone during light flecks; (b) these characteristics were associated with phase III CO_2 fixation of CAM; (c) when grown in full sun, *A. magdalenae* was chronically photoinhibited despite a remarkably high nonphotochemical quenching capacity, indicating a large potential for photoprotection; and (d) the degree of photoinhibition was inversely proportional to the length of phase III. Results from the light fleck studies suggest that understory *A. magdalenae* plants can make more efficient use of sun flecks for leaf carbon gain over most of the day than co-occurring C_3 species. The association between the duration of phase III and the degree of photoinhibition for *A. magdalenae* in high light is discussed in relation to the limited photosynthetic plasticity in this species.**

Our understanding of the potential value of CAM for plant carbon gain is based largely on studies of desert succulents and upper canopy epiphytes from tropical forests (Winter and Smith, 1996). When taken together, the phylogeny, biogeography, and physiology of CAM plants provide compelling evidence for the ecological significance of this photosynthetic pathway in sun-exposed, water-limited habitats (Osmond, 1978; Winter, 1985; Lüttge, 1987; Griffiths, 1988; Smith, 1989). Nocturnal CO_2 uptake coupled with stomatal closure during the day maximizes the ratio of carbon gain to water loss (Nobel, 1976). High daytime partial pressures of CO_2 inside the leaf help to mitigate the photoinhibitory effects of high light common to these environments (Osmond, 1982; Adams and Osmond, 1988). The capacity to maintain a functioning photosynthetic apparatus by re-fixation of respired CO_2 when stomates are continuously closed during prolonged drought helps CAM plants to survive in exposed, xeric sites (Szarek et al., 1973; Griffiths et al., 1989). Although uncommon, the occurrence of CAM in terrestrial plants growing in moist, shaded habitats is well documented (Medina, 1987). It is, however, unclear what the functional significance of constitutive CAM may be among terrestrial plants in these low light, mesic habitats.

Aechmea magdalenae André ex Baker is a large (≤2 m tall), terrestrial bromeliad widely distributed between Mexico and Ecuador (Croat, 1978). Over its geographical range, populations of this species occur locally in dry, exposed sites and, more remarkably for a terrestrial CAM plant, in moist, low light sites. In the rain forest understory of central Panama, this species forms dense clonal thickets and may actually dominate large portions of the local forest floor (Brokaw, 1983; Pfitsch and Smith, 1988; Murawski and Hamrick, 1990). Populations of this plant in Panamanian rain forests are typically found in extremely low light sites, often adjacent to lakes or streams, and presumably only experience high light stress or water limitations on rare occasions. Moreover, Pfitsch and Smith (1988) demonstrated over a broad range of light and moisture conditions that this species always does the majority of its daily carbon uptake during the night, i.e. *A. magdalenae* expresses CAM constitutively. These observations indicate that constitutive CAM photosynthesis per se does not preclude the survival and growth of these plants in low light, mesic habitats.

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Abbreviations: BCI, Barro Colorado Island; F, actual fluorescence in actinic light; $\Delta F/F_m'$, actual photochemical efficiency of PSII, where $\Delta F = F_m' - F$; F_m (F_m'), maximum fluorescence in the absence (presence) of thylakoid energization, respectively; F_o (F_o'), minimum fluorescence in the absence (presence) of thylakoid energization, respectively; F_v/F_m, maximum photochemical efficiency of PSII, where $F_v = F_m - F_o$; HL, high-light; LL, low-light; NPQ, nonphotochemical quenching of PSII chlorophyll fluorescence; Q, plastoquinone; qP, photochemical quenching of PSII chlorophyll fluorescence; 1 − qP, reduction state of the plastoquinone pool.

It has also been shown that the light- and CO_2-saturated rate of photosynthetic oxygen evolution on a leaf area or nitrogen basis in *A. magdalenae* is substantially greater than that of co-occurring C_3 understory species from central Panama (Königer et al., 1995). Furthermore, there is evidence that a high photosynthetic capacity, which is potentially advantageous for carbon gain during sun flecks, might be a general characteristic of shade-tolerant, terrestrial CAM bromeliads. High maximum rates of photosynthesis have been observed in shade-grown *Bromelia humilis*, a terrestrial CAM bromeliad from northern Venezuela (Fetene et al., 1990), as well as in *Bromelia karatas* and *Ananas comosus* from Panamanian rain forests (J.B. Skillman, unpublished data). Additionally, there is evidence that these species do not photosynthetically acclimate to different light conditions with adjustments in the maximum photosynthesis rate to the extent typically observed in higher plants. Maximum photosynthesis rates were similar in high light- and low light-grown *B. humilis* (Fetene et al., 1990) and in high light- and low light-grown *A. magdalenae* (J.B. Skillman, unpublished data). These observations challenge conventional views regarding (a) the ecological significance of CAM and (b) the relationship between maximum rates of photosynthesis and the light environment a plant inhabits.

The overall aim of this study was to characterize how light affects daytime photosynthetic physiology in vivo in this unusual shade-tolerant CAM plant. Studies of leaf photosynthesis by conventional gas-exchange techniques are of limited use in CAM plants due to stomatal closure during phase III (Osmond, 1978; the daytime de-acidification portion of the CAM cycle). Modern chlorophyll fluorescence methods (reviewed by Schreiber et al., 1994) have proven to be of great use in CAM research (Winter and Demmig, 1987; Winter et al., 1990; Keiller et al., 1994; Adams and Demmig-Adams, 1996) and were used in this study to examine photosynthetic responses to various environmental and physiological factors in *A. magdalenae* and associated C_3 species. Specific objectives were (a) to investigate the proposal that a high photosynthetic capacity in *A. magdalenae* enables this species to use sun flecks more efficiently for daytime CO_2 fixation than co-occurring C_3 shade plants; (b) to explore the influence of growth irradiance and time of day (as a proxy of CAM phase) on photochemical efficiency and nonphotochemical quenching, and (c) to assess the influence of current ambient light level and the growth irradiance history on the daytime CAM cycle dynamics and the susceptibility to photoinhibition in *A. magdalenae*.

MATERIALS AND METHODS

These studies were conducted on BCI in central Panama (9°10′ N, 79°51′ W), which has an annual precipitation of approximately 2600 mm and distinct wet (May to December) and dry seasons (January to April). The island is covered by semideciduous tropical forest. Detailed descriptions of vegetation, climate, and ecology of the island can be found in Croat (1978) and Leigh et al. (1996).

Plant Material and Experimental Conditions

Results are presented from three studies on the photosynthetic ecophysiology of *Aechmea magdalenae* André ex Baker. First, we evaluated the in situ photosynthetic responses to light flecks in noninduced leaves on plants growing in the understory on BCI. For this study, six common understory plant species (listed in Table I) were selected to represent a wide range of higher plant taxa and growth forms. With the exception of *A. magdalenae*, all selected species use the C_3 photosynthetic pathway. Responses to light flecks were assessed on understory plants early in the day (between 9 AM and 1 PM local time) during the wet season. At this time stomatal limitations on photosynthesis in the C_3 plants were expected to have been slight and the CAM plants were expected to have been in phase III.

Next, a shadehouse experiment was designed to examine the influence of growth irradiance on photosynthetic physiology in *A. magdalenae*. For this study, juvenile plants of *A. magdalenae* and the sympatric C_3 monocot herb, *Dieffenbachia longispatha* Engler and Krause, were transplanted from the forest in November 1994 to a 1:2 mixture of sand and forest soil. They were allowed to establish in low light (5–10% of full sun) in a screened growing house on BCI. Plants received natural rainfall, were watered as needed, and received commercial 10–10-10 (N, P, K) nutrient fertilizer at a rate of 500 mL once a week during establishment and throughout the experiment. In April 1995, plants were transplanted to 19-L pots with the same soil mixture and randomly transferred to one of two light treatments in a clearing near the BCI laboratories. Neutral-density shade fabric was used to impose the LL treatment. Plants in the HL treatment were exposed to natural daylight. An electronic data logger and calibrated quantum sensors (model 190s, Li Cor, Lincoln, NE) were used to characterize the treatment light levels during the duration of the experiment. Mean daily irradiances during the entire 5-month experiment were 21.01 ± 0.95 (100% full sun) and 0.17 ± 0.01 (1% full sun) mol m^{-2} d^{-1} PPFD for the HL and LL treatments, respectively.

Finally, a growth chamber experiment was designed to examine the influence of the growth irradiance history on photochemical efficiency and daytime CAM activity under a constant environment of contrasting ambient light levels. During September 1995, a subset of HL and LL plants were placed one at a time in a controlled environment chamber

Table I. *Description of the understory species used in the light-fleck studies*

Taxonomic nomenclature is based on Croat (1978).

Species	Family	Growth Form	Photosynthetic Pathway
Aechmea magdalenae	Bromeliaceae	Herb	CAM
Alseis blackiana	Rubiaceae	Tree	C3
Dieffenbachia longispatha	Araceae	Herb	C3
Pharus latifolia	Gramineae	Herb	C3
Piper cordulatum	Piperaceae	Shrub	C3
Psychotria marginata	Rubiaceae	Shrub	C3

(EGC, Chagrin Falls, OH) for 24 h. Each plant was placed in the chamber after sunset the evening before the measurements were to be made. Set points in the chamber were as follows: 12-h day, 30°C, and 80% RH, and 12-h night, 25°C, and 80% RH. Light incident on the measured leaf was controlled by adjusting the chamber height of the plant and by the use of a chamber insert lined with neutral-density shade fabric. Light incident on measured leaves in the high light chamber treatment was 316.1 ± 1.7 μmol m^{-2} s^{-1} PPFD, with an average daytime leaf temperature of 31.0 ± 0.1°C. Light incident on measured leaves in the low light chamber treatment was 64.4 ± 0.3 μmol m^{-2} s^{-1} PPFD, with an average daytime leaf temperature of 29.6 ± 0.1°C. In all studies, measurements were made on intact, new, fully enlarged leaves that had developed under the given growth regime. Comparative fluorescence measurements were always taken from the same region of the leaf for a given species.

Chlorophyll Fluorescence Measurements

Chlorophyll fluorescence measurements were made with a field-portable fluorometer (PAM-2000, Walz, Effeltrich, Germany). Saturating pulses for the determination of F_m and F_m' were >5000 μmol m^{-2} s^{-1} PPFD and were 800 ms in duration, which was sufficient to achieve a stable maximum fluorescence yield. In cases in which F_o' was determined, the leaf was quickly darkened with a black cloth immediately after determination of F_m' and then illuminated with far-red light for 15 s. The measuring beam frequency was set to 600 Hz with the auto-20 kHz option engaged. In all cases, leaves were dark-adapted for a minimum of 15 min prior to determinations of F_v/F_m. qP was calculated as described by van Kooten and Snel (1990), where 1 − qP is interpreted as an index of the excitation pressure on PSII. NPQ was calculated as NPQ = F_m/F_m' − 1 and is interpreted as an index of excitation dissipation from the light-harvesting pigment bed (Bilger and Björkman, 1990). The photochemical efficiency of noncyclic PSII electron transport ($\Delta F/F_m'$) was calculated as in Genty et al. (1989). The relative rate of PSII electron flux is indicated by the product of $\Delta F/F_m'$ and PPFD. Reported light-saturated values of $\Delta F/F_m'$ × PPFD as an index of the maximum photosynthesis rate are based on the best fit of the light-response data against the Smith equation (Smith, 1937).

Controlled light-response studies (steady state or light fleck) were made using a variable intensity quartz halogen lamp mounted on the fluorometer leaf clip. The light was filtered to minimize heating of the leaf. Leaf temperature and light incident on the leaf were monitored using the leaf thermocouple and microquantum sensor incorporated into the fluorometer leaf clip. The microquantum sensor was frequently calibrated against a quantum sensor (model 190, Li Cor), which had been recently factory-calibrated.

On the evening before the controlled light fleck-response studies, small shade tents were placed 20 to 100 cm above selected leaves to prevent the interception of direct sun prior to the experiment. The next morning, shaded, noninduced leaves were exposed to one of two different light exposure regimes: 300 μmol m^{-2} s^{-1} PPFD for 6 min (6:300) or 1500 μmol m^{-2} s^{-1} PPFD for 30 min (30:1500). Based on preliminary work on the study species, fluorescence measurements during the simulated sun fleck were scheduled to maximize the amount of information that could be determined for the initial response to the step increase in light without the saturating pulse itself influencing subsequent measured fluorescence yields or the trajectory of the induction response. Fluorescence parameters were determined at 1, 2, 4, and 6 min for both experimental light fleck protocols. Additional determinations were made at 14, 22, and 30 min for the 30:1500 light flecks.

In the growth chamber studies, two dark-adapted F_v/F_m determinations were made. A pre-photoperiod point was taken 10 min prior to the chamber lights coming on in the morning and a post-photoperiod point was taken 1 h after the chamber lights went off at night. During the course of the 12-h photoperiod, saturating pulses were applied and fluorescence data were collected at 10-min intervals.

Statistical Analyses

When the objective was to examine the influence of growth irradiance on physiological parameters, treatment differences were inferred using a Student's *t* test (Steel and Torrie, 1980). When the objective was to examine the influences and interactive effects of growth irradiance and the ambient light level on physiological parameters, treatment differences were inferred using two-way analysis of variance and Scheffé means comparison tests (Steel and Torrie, 1980). Data sets were checked for homogeneity of variance and, when necessary, log-transformed prior to running statistical models. All reported measures of variation are SES.

RESULTS

Photosynthetic Electron Transport Responses to Increasing Light: Steady-State and Light Flecks

Chlorophyll fluorescence was used to examine in situ photosynthetic responses to increasing light on selected individuals of the species listed in Table I. The relative light-saturated rate of PSII electron flux under steady-state conditions was considerably higher in the understory CAM plant *A. magdalenae* than in typical understory C_3 plants (Fig. 1). This is consistent with results from steady-state photosynthetic oxygen evolution measurements (Königer et al., 1995). In the absence of any unique induction limitations, high maximum rates of photosynthesis and electron transport in *A. magdalenae* should allow this shade CAM plant to make greater use of sun flecks for leaf carbon gain than more typical shade plants.

Photosynthetic responses to controlled light fleck regimes (6:300 and 30:1500) were examined in situ on noninduced leaves from the species listed in Table I (Fig. 2). There were no detectable species differences in the relative rate of PSII electron transport at 15 μmol m^{-2} s^{-1} PPFD (comparable to daytime diffuse irradiances in the understory). During experimental light flecks, the relative rate of PSII electron transport in *A. magdalenae* was higher than that observed in sympatric C_3 species. This is consistent with steady-state light-response measurements (Fig. 1) in-

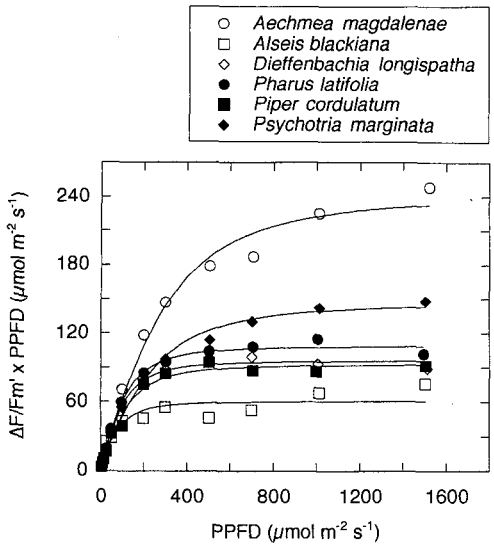

Figure 1. Representative light-response curves of $\Delta F/F_m' \times$ PPFD, an index of PSII electron transport, for the six study species. All measurements were made on intact leaves on plants in the forest.

dicating no special induction lags in *A. magdalenae*. To the contrary, the dynamic response in shaded leaves to the 6:300 light fleck indicated that photosynthetic electron transport in *A. magdalenae* was fully induced 1 min after the increase in light (Fig. 2A). In general, understory C_3 species had not attained steady-state rates even after 6 min at the higher PPFD. Similar results were obtained in follow-up studies for longer light flecks of 300 μmol m^{-2} s^{-1} PPFD. It was found that 1 min after the step increase in PPFD, understory C_3 species had attained between only 65 and 80% of the full induction state, whereas *A. magdalenae* had already attained 95 to 100% (data not shown). These same species differences in the induction rate were not observed in response to the 30:1500 light fleck (Fig. 2B). *A. magdalenae* and the C_3 species alike required approximately 5 to 10 min to attain steady-state rates at this higher light level.

Fate of Excess Light: the Interplay between PSII Closure and Energy Dissipation

A time course of the interactive response of 1 − qP and NPQ is shown for the six understory species over the experimental 30-min light fleck (Fig. 3). High values of 1 − qP are indicative of overreduction of the Q pool, a prerequisite for PSII damage/inactivation (Krause, 1988; Demmig-Adams and Adams, 1992; Osmond, 1994). High values of NPQ are indicative of the engagement of processes that function in the regulated dissipation of excess excitation energy, effectively mitigating photodamage/inactivation (Krause, 1988; Demmig-Adams and Adams, 1992; Osmond, 1994).

Qualitatively, the response to the light fleck was the same for *A. magdalenae* as it was for the other understory plants. In all species, 1 min after the step increase from 15 to 1500 μmol m^{-2} s^{-1} PPFD, a large fraction of the PSII centers were closed. In all species as the light fleck proceeded, there was increasing engagement of dissipative processes (increase in NPQ) and a partial re-oxidation of the Q pool (decrease in 1 − qP). For CAM and C_3 plants alike, the greatest rate of change in both 1 − qP and NPQ occurred during the first 5 to 10 min of the 30-min light fleck, which was coincident with the increase in the overall rate of linear electron transport (Fig. 2B). Despite the similarities, there were clear quantitative differences between *A. magdalenae* and the C_3 understory species in the response of 1 − qP and NPQ to the light fleck. The C_3 species all converged on an apparent equilibrium NPQ value, which was 10 to 20% greater than that of *A. magdalenae*. Compared with the C_3 species, the reduction state of the Q pool in *A. magdalenae* was lower at each time-point during the course of the light fleck. Dark-adapted F_v/F_m values after the 30:1500 light fleck experiment were, on average, 13.5% lower in the C_3 species and 10.8% lower in *A. magdalenae* compared with measurements made prior to the light fleck (data not shown).

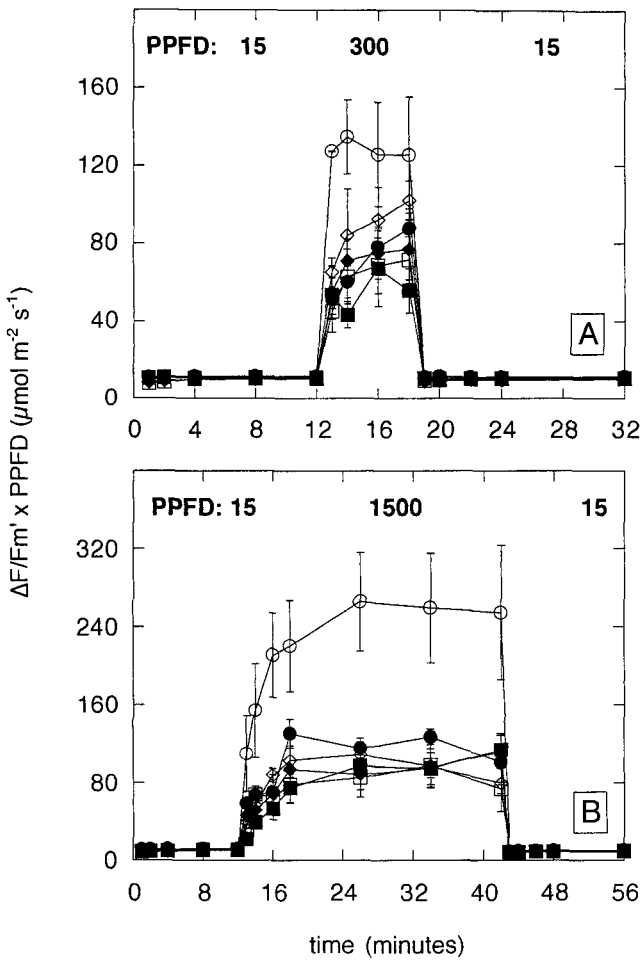

Figure 2. Response of $\Delta F/F_m' \times$ PPFD, an index of PSII electron transport, to controlled light fleck regimes in noninduced leaves. At time 0 the light was switched on (15 μmol m^{-2} s^{-1} PPFD). Light was increased at 12 min to 300 μmol m^{-2} s^{-1} PPFD for 6 min (A) or 1500 μmol m^{-2} s^{-1} PPFD for 30 min (B). Light was decreased to 15 μmol m^{-2} s^{-1} PPFD after the light fleck. Results are the means ± SE of three to four leaves. All measurements were made on intact leaves on plants in the forest. Symbols are as defined in Figure 1.

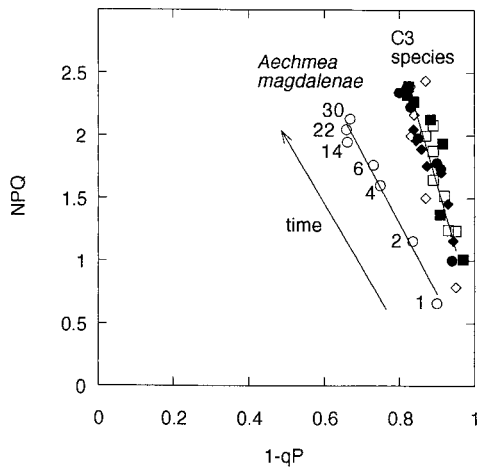

Figure 3. Time-course response of 1 − qP and NPQ during a 30-min light fleck at 1500 μmol m^{-2} s^{-1} PPFD in noninduced leaves. The arrow indicates the direction of the time course. The numbers next to the *A. magdalenae* data points are the time in minutes after the step increase in light from 15 to 1500 μmol m^{-2} s^{-1} PPFD. Results are the means ± SE of three to four leaves. Measurement conditions and protocol are as in Figure 2B. Symbols are as defined in Figure 1.

Influence of Growth Irradiance and CAM Phases on Photosynthetic Electron Transport, Susceptibility to Photoinhibition, and the Capacity for Energy Dissipation

The influences of growth irradiance (HL versus LL) and time of day (early versus late) on the relative rate of PSII electron flux were examined for *A. magdalenae* and the C_3 herb *D. longispatha* (Fig. 4). To accomplish this, both species were grown for several months under contrasting light environments of 1% (LL) and 100% (HL) full sun. The time of day during which measurements were made had a large effect on the maximum rate in *A. magdalenae* but not in *D. longispatha*. Consequently, results from *D. longispatha* are presented without regard to the time of day that the data were collected (Fig. 4A). Results from *A. magdalenae* are presented separately for measurements made early (i.e. between 9 AM and 1 PM local time) and those made late (i.e. between 3 and 6 PM local time) in the day (Fig. 4, B and C).

Among low light-grown plants from either the forest or the LL shadehouse treatment, the maximum PSII electron flux was higher in LL shadehouse plants than it was in forest plants of the same species (cf. Fig. 1 with Fig. 4, A and B). However, in the morning, relative species differences among LL shadehouse-grown plants were comparable to those of forest-grown plants. In both low light environments (forest and shadehouse), the maximum morning rate for *A. magdalenae* was more than twice that of *D. longispatha*. Within a shade-house growth regime (HL or LL), maximum rates in *A. magdalenae* late in the day were similar to or lower than those in *D. longispatha*. Thus, the light-saturated rate of photosynthesis observed in *A. magdalenae* appears to depend on what phase of the CAM cycle the plant is in. In *D. longispatha*, maximum rates among HL plants were significantly higher than among LL plants (Student's *t* test; P = 0.0009). In *A. magdalenae*, higher maximum rates were observed in LL compared with HL plants. These differences were not statistically significant, however, for either morning (Student's *t* test; P = 0.8401) or late afternoon (Student's *t* test; P = 0.2799) measurements.

The influences of growth irradiance (HL versus LL) and time of day (early versus late) on the capacity for the dissipation of excess excitation energy were examined for both species (Fig. 5). As above, there was little effect of measurement time on NPQ in *D. longispatha*, and results for this species are presented without regard to the time of day (Fig. 5A). For either species, compared with LL plants, HL plants had a greater capacity for dissipation of excess energy, as evidenced by the higher light-saturated NPQ values (Fig. 5). Growth irradiance effects on NPQ in *D. longispatha* measured at 1500 μmol m^{-2} s^{-1} PPFD (NPQ_{1500}) were highly significant (Student's *t* test; P = 0.0013) (Fig.

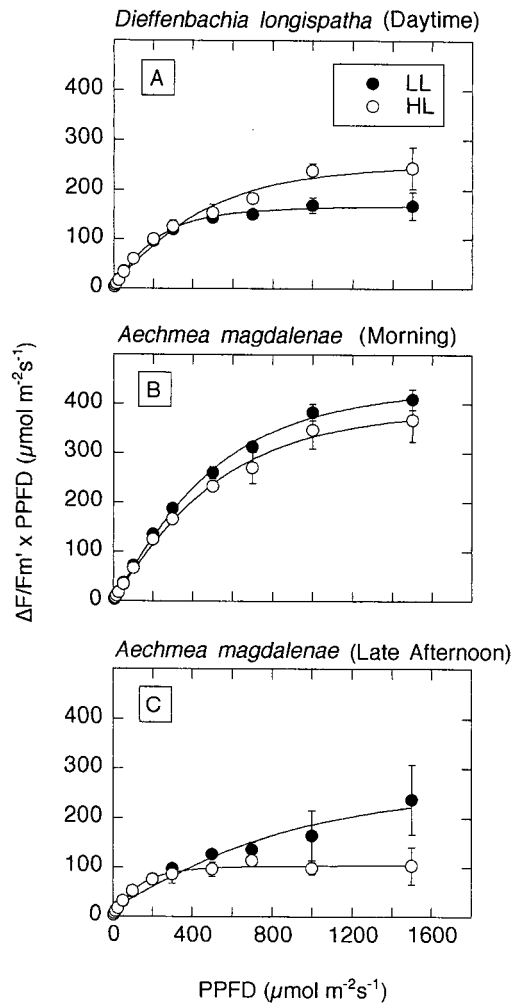

Figure 4. Light-response curves of $\Delta F/F_m' \times$ PPFD, an index of PSII electron transport, for plants grown in 1% (LL) and 100% (HL) of full sun. Data for *D. longispatha* (A) are pooled from measurements made at various times during the day. Data for *A. magdalenae* in the "morning" (B) are from measurements made before 1 PM local time. Data for *A. magdalenae* in the "late afternoon" (C) are from measurements made between 3 and 6 PM local time. Results are means ± SE of three leaves. All measurements were made on intact leaves on plants in the growing house.

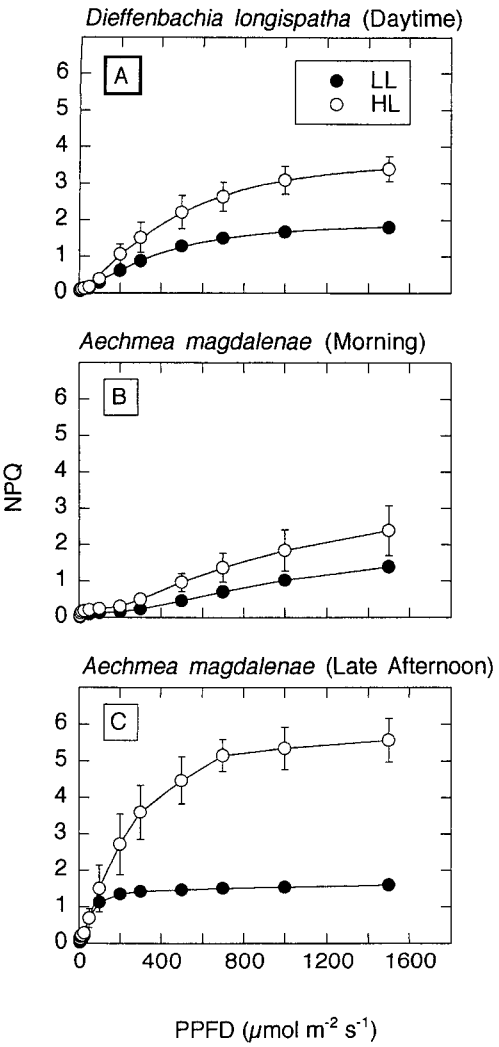

Figure 5. Light-response curves of NPQ. A, *D. longispatha* in the daytime. B, *A. magdalenae* early in the day. C, *A. magdalenae* late in the day. Measurement conditions and protocol are as in Figure 4. Results are means ± SE of three leaves.

5A). There was differential engagement of dissipation processes in *A. magdalenae*, depending on the time of day that measurements were made (Fig. 5, B and C). In the morning, NPQ_{1500} in LL leaves was not significantly different from NPQ_{1500} in HL leaves (Student's *t* test; P = 0.5485). By contrast, differences in NPQ_{1500} between LL leaves and HL leaves measured later in the day were highly significant (Student's *t* test; P = 0.0003). In the early part of the day there was no indication of light saturation of NPQ for *A. magdalenae* plants over the range of PPFDs evaluated (Fig. 5B). Late afternoon measurements on the same plants indicated that NPQ was light-saturated at 100 to 200 μmol m^{-2} s^{-1} PPFD in the LL plants and at approximately 700 μmol m^{-2} s^{-1} PPFD in the HL plants (Fig. 5C).

The influence of growth irradiance (HL versus LL) and the growth chamber light level (64 versus 316 μmol m^{-2} s^{-1} PPFD) on the maximum photochemical efficiency (F_v/F_m) and the degree of photoinhibition resulting from the chamber treatment were examined for *A. magdalenae* (Table II). Dark-adapted F_v/F_m values in the morning, before the chamber lights came on, were lower in HL plants than they were in LL plants. After 12 h under contrasting light levels and 1 h in the dark, F_v/F_m was significantly lower in *A. magdalenae* plants that had been in the high light chamber compared with those that had been in the low light chamber (Table II). The relative decline in the maximum photochemical efficiency in response to the growth chamber light level, as an indication of the severity of photoinhibition, was affected by both the light level in the chamber and the growth light regime (Table II). In *A. magdalenae* under a given ambient light level, HL plants were consistently less photoinhibited than LL plants. The relative loss in photochemical efficiency was always greatest under the higher growth chamber light level. It is noteworthy that in the low light growth chamber treatment, chronically photoinhibited HL *A. magdalenae* plants were unaffected or actually recovered slightly.

The influences of growth irradiance (HL versus LL) and the growth chamber light level (64 versus 316 μmol m^{-2} s^{-1} PPFD) on PSII efficiency and nonphotochemical quenching were explored for *A. magdalenae* and *D. longispatha* over a 12-h day of constant environmental conditions (Figs. 6 and 7). In *D. longispatha*, over the course of a controlled 12-h day, there was a gradual decline in the efficiency of PSII electron transport ($\Delta F/F_m'$; Fig. 6, A and B), coinciding with a slow increase in NPQ (Fig. 6, C and D). There was little variation over time in either $\Delta F/F_m'$ or NPQ in this species, regardless of the growth treatment or the ambient light conditions. The pattern in Figure 6 is largely consistent with predictions based on steady-state light-response measurements in Figures 4A and 5A.

In *A. magdalenae*, over the course of a controlled 12-h day, there was large variation in the efficiency of PSII

Table II. *Maximum photochemical efficiency (F_v/F_m) before and after a 12-h photoperiod of constant irradiance of approximately 64 or 316 μmol m^{-2} s^{-1} PPFD for A. magdalenae plants grown in 100% (HL) or 1% (LL) full sun*

Pre-photoperiod measurements were made prior to the chamber lights coming on with plants that had been in the darkened growth chamber for 10 to 12 h. Post-photoperiod measurements were made 1 h after the chamber lights had gone off, i.e. 1 h of dark adaptation/recovery. Values are means (±1 SE; *n* = 3); different superscripts within a column indicate means that differed at P < 0.05 by Scheffé means comparison test.

Growth Chamber Light Level	Growth Light Regime	Pre-Photoperiod F_v/F_m	Post-Photoperiod F_v/F_m	% Reduction of F_v/F_m
64 μmol m^{-2} s^{-1}	LL	0.786[a] (0.002)	0.738[a] (0.013)	6.1[a] (1.7)
	HL	0.745[b] (0.003)	0.746[a] (0.007)	−0.1[b] (0.7)
316 μmol m^{-2} s^{-1}	LL	0.782[a] (0.003)	0.618[b] (0.015)	21.0[c] (1.6)
	HL	0.747[b] (0.012)	0.657[b] (0.021)	12.1[d] (1.4)

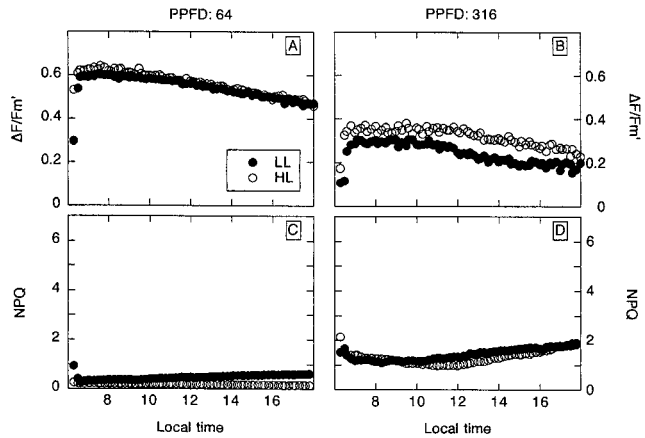

Figure 6. Response of $\Delta F/F_m'$ (A and B) and NPQ (C and D) in *D. longispatha* grown in 1% (LL) or 100% (HL) full sun to 12-h photoperiod of constant irradiance of approximately 64 (A and C) or 316 (B and D) μmol m^{-2} s^{-1} PPFD. Measurements were made every 10 min on intact leaves of plants in the growth chamber.

electron transport ($\Delta F/F_m'$; Fig. 7, A and B) and the degree of energy dissipation (NPQ; Fig. 7, C and D). The temporal variation in fluorescence parameters reflects the different daytime CAM phases. These studies gave consistent evidence for the expression of three CAM phases during the day in the HL plants (phases II, III, and IV), but there was little or no expression of phase II in LL plants under either chamber light level. Many aspects of the results shown in Figure 7, including the magnitude of variation over time, the influence of growth irradiance, and the influence of chamber irradiance levels, are consistent with predictions based on steady-state light-response measurements in Figures 4, B and C, and 5, B and C. What is not predictable from steady-state light-response curves is the apparent duration of the different CAM phases and the influence that growth irradiance and ambient light treatments had on this variable. To accomplish this, the high-efficiency phase was defined as the time during the day when $\Delta F/F_m'$ was within 25% of the peak recorded for a given leaf (Table III). (The 25% threshold value was somewhat arbitrary in that qualitatively similar results were obtained with other threshold values.) Table III indicates that the portion of the day that photosynthesis was CO_2-saturated, or nearly so, by the de-carboxylation of nocturnally accumulated malic acid depended on the current (chamber) light level and the previous light history of the plant (HL versus LL). Compared with the high light chamber treatment, the low light chamber treatment extended the portion of the day plants were in the high-efficiency, CO_2-saturated phase. At a given chamber light level, the duration of this high-efficiency phase was significantly shorter in LL-grown plants compared with HL-grown plants.

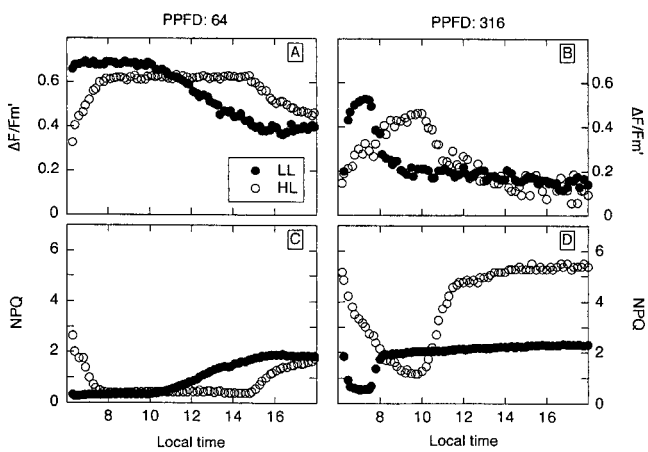

Figure 7. Response of $\Delta F/F_m'$ (A and B) and NPQ (C and D) in *A. magdalenae* grown in 1% (LL) or 100% (HL) full sun to 12-h photoperiod of constant irradiance of approximately 64 (A and C) or 316 (B and D) μmol m^{-2} s^{-1} PPFD. Measurements were made every 10 min on intact leaves of plants in the growth chamber.

Data in Tables II and III suggest a functional relationship between the apparent duration of the CO_2-saturated CAM phase over a 12-h day of constant irradiance and the degree of photoinhibition at the end of that day (Fig. 8). A long period of high-efficiency, CO_2-saturated photosynthesis will result from either (a) light-limited rates of CO_2 assimilation and malate consumption or (b) in saturating-light, abundant malate supplies capable of supporting maximum rates of photosynthesis for an extensive portion of the day. Given this interpretation, the relationship shown in Figure 8 suggests that the balance between the rate of malate consumption and malate supply determines how susceptible to photoinhibition *A. magdalenae* will be under high light conditions.

DISCUSSION

Photosynthetic Electron Transport Responses to Increasing Light: Steady-State and Light Flecks

Shade-grown *A. magdalenae* has consistently been found to have a higher maximum photosynthesis rate than is typically observed for shade-grown plants (Königer et al., 1995; J.B. Skillman, unpublished data). Results presented here are corroborative because they demonstrate that during the morning low light-grown *A. magdalenae* has a light-saturated rate of PSII electron transport well in excess of that observed for LL-grown sympatric C_3 species (Figs. 1, 2, and 4). It is

Table III. *Duration of high photochemical efficiency phase during a 12-h photoperiod of constant irradiance (approximately 64 or 316 μmol m^{-2} s^{-1} PPFD) for A. magdalenae plants grown in 100% (HL) or 1% (LL) full sun*

Values are the mean (±1 SE; n = 3) number of hours each day when $\Delta F/F_m'$ was within 25% of the peak value measured on a plant during the 12-h chamber day and corresponds approximately to the duration of the malate decarboxylation phase of CAM. Different superscripts indicate means that differed at $P < 0.05$ by Scheffé mean comparison test.

Growth Light Regime	Growth Chamber Light Level	
	64 μmol m^{-2} s^{-1} PPFD	316 μmol m^{-2} s^{-1} PPFD
	h	*h*
LL	7.06[a] (0.47)	1.56[b] (0.24)
HL	10.89[c] (0.57)	2.95[d] (0.14)

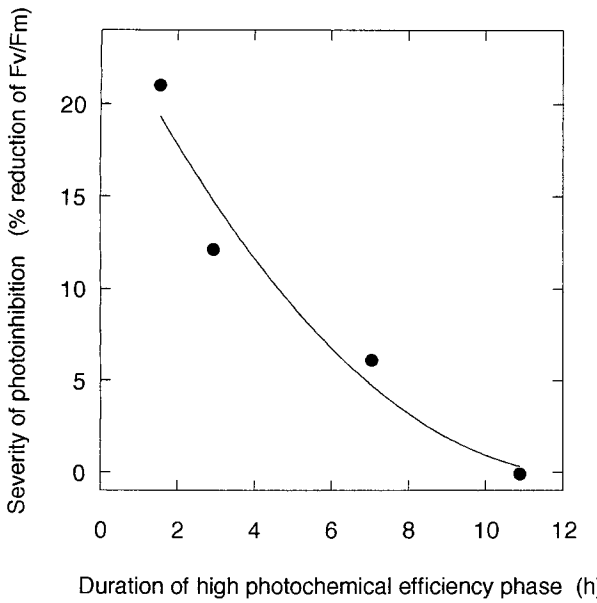

Figure 8. Relationship between the duration of the high photochemical efficiency phase (an index of the length of CAM phase III) in *A. magdalenae* and the severity of photoinhibition from a known 12-h light dose. Each point is mean of three independent observations. Data are from Tables II and III.

worth recalling that for C_3 plants in air as much as half of the photochemically generated assimilatory power is diverted from carbon fixation to photorespiratory reactions. Consequently, differences in the light-saturated rate of carbon assimilation between *A. magdalenae* and a typical understory C_3 species are expected to be even greater than those observed for photosynthetic electron flux.

From the perspective of a cost-benefit analysis it is unclear why, in the shade, *A. magdalenae* (and at least some other understory constitutive CAM species) produces the metabolic apparatus capable of a high maximum photosynthesis rate. Although this trait may be advantageous during sun flecks, this benefit alone is unlikely to offset the resource requirements of a high-activity photosynthetic apparatus in a light-limited habitat; otherwise, this would be expected to be a common character among understory plants. During phase III, *A. magdalenae* in the forest may be able to make efficient use of a high photosynthetic capacity in sun flecks because it has a rapid induction response and because the substrate CO_2 supply is high during this phase of the CAM cycle. Under naturally fluctuating light conditions in the understory, it is conceivable that this combination of a fast induction response with a high photosynthesis rate and a high substrate supply partially offsets the resource requirements of producing and maintaining the metabolic machinery necessary to achieve that high rate. Moreover, the leaf nitrogen concentration is quite low in *A. magdalenae* (Königer et al., 1995), suggesting that resource requirements for a high-capacity photosynthetic apparatus in this CAM species are relatively low.

The mechanistic basis of the observed differences in induction rate is unknown (Fig. 2). Pearcy and co-workers have identified and characterized the factors contributing to induction limitations in leaves of C_3 plants (reviewed by Pearcy et al., 1994). Their findings indicate that the rate of Rubisco activation dominates the induction response for the period of approximately 1 to 10 min following a step increase in light, which is consistent with the kinetics observed in Figure 2. Rubisco activation as a limiting step for PSII electron flux is also concordant with our understanding of the coordinated regulation of different components of the photosynthetic apparatus. Following an increase in light, a low Rubisco activation state limits assimilatory power use in both carbon assimilation and photorespiration; this in turn feeds back to down-regulate PSII electron transport as monitored by chlorophyll fluorescence (Sharkey et al., 1988). Little is known about the regulation of Rubisco in CAM plants. Our findings suggest that the high intercellular partial pressures of CO_2 characteristic of CAM phase III result in a high Rubisco activation state even in low light. The basis of the differential induction response in *A. magdalenae*, depending on the light fleck intensity, is also unknown. This may reflect different processes that limit Rubisco activation in response to an increase in PPFD, depending on the magnitude of the increase in light (Woodrow et al., 1996).

Fate of Excess Light: the Interplay between PSII Closure and Energy Dissipation

The 30:1500 light fleck was viewed as potentially photoinhibitory in these understory plants. The results shown in Figure 3 are consistent with the idea that a higher photosynthetic activity helps to minimize the overreduction of the Q pool in high light and that photoprotective processes will be engaged to a lesser extent. Consequently, even in the absence of a greater potential for the dissipation of excess excitation energy, forest-grown *A. magdalenae* would be expected to be less susceptible to light-induced losses in PSII function during bright sun flecks compared with other understory plants. Comparisons of the pre- and post-light fleck F_v/F_m values indicated that, indeed, the 30:1500 light fleck was photoinhibitory; however, as expected from the behavior of 1 − qP, the F_v/F_m decline in the C_3 species was greater than in *A. magdalenae*.

Influence of Growth Irradiance and CAM Phases on Photosynthetic Electron Transport, Susceptibility to Photoinhibition, and the Capacity for Energy Dissipation

Despite having relatively high maximum rates of PSII electron transport and photosynthesis and an extremely high potential for the dissipation of excess light, *A. magdalenae* sustained a modest level of chronic photoinhibition when growing in high light (Table II). Thus, in *A. magdalenae* over the day in full sun, the amount of absorbed light was greater than that which could be safely dissipated or used in photosynthetic metabolism. This may, in part, be attributable to the influence of the different daytime CAM phases on photochemical efficiency. Limiting CO_2 during phases II and IV in full sun might result in PSII damage/inactivation. In addition, leaves on bromeliad rosettes are constrained to a narrow range of leaf orientations. Consequently, *A. magdalenae* is unable to avoid high irradiance loads by paraheliotropism.

On the other hand, the capacity for avoiding high light stress by energy dissipation from the thylakoid pigment bed is highly developed in this CAM species. The light-saturated NPQ value of approximately 5.5 in HL *A. magdalenae* (late in the day) was nearly double that of *D. longispatha* growing under the same conditions (Fig. 5). It is also considerably higher than the maximum NPQ values of 3 to 4 typically reported for high light grown plants (Bilger and Björkman, 1990, 1991; Osmond et al., 1993; Ruban et al., 1993; Demmig-Adams and Adams, 1994; Bilger et al., 1995; Adams and Demmig-Adams, 1996; Shen et al., 1996). From this literature it is believed that sun-adapted species have a greater maximum potential for nonphotochemical energy dissipation than shade-adapted species when both are grown in high light (Thayer and Björkman, 1990; Demmig-Adams and Adams, 1994). Therefore, we did not expect *A. magdalenae*, a plant tolerant of extreme shade, to have one of the highest reported light saturated values of NPQ. This observation is remarkable even when recognizing that this species also occurs in more exposed sites. It is interesting that *Guzmania monostachia*, an epiphytic bromeliad, has a similarly high maximum NPQ when grown in high light (Ruban et al., 1993). An especially high potential for the regulated dissipation of excess light may be characteristic of photosynthetic organisms that undergo rapid changes in the level of environmental light stress on a daily basis, a time scale that is too short for coarse control acclimation responses. Alternatively, a large capacity for NPQ-related energy dissipation may be phylogenetically conserved among bromeliads.

In *A. magdalenae*, the susceptibility to photoinhibition was inversely related to the duration of phase III (Fig. 8). This relationship suggests that during the day the degree of photoinhibition in *A. magdalenae*, and perhaps other CAM plants, is directly related to the rate of malate consumption and inversely related to the malate pool size. It will be interesting to find out whether this relationship has any bearing on the apparent absence of photosynthetic light acclimation in this species. Under light-saturating conditions, an acclimatory increase in the photosynthetic capacity would presumably increase the consumption rate of nocturnally accumulated malic acid, shortening phase III and increasing the portion of the day that the leaf was CO_2-limited. Paradoxically, this implies that in high light an increase in the photosynthetic capacity without a proportional increase in the malate supply might lead to an increased risk of photoinhibition in CAM plants. Notably, there is evidence that in *A. magdalenae* the amount of nocturnally fixed malate in HL-grown plants is similar to that in LL plants.

From gas-exchange studies, Pfitsch and Smith (1988) found that there was no significant difference in the amount of nocturnal carbon fixed in *A. magdalenae* plants grown in 5 and 35% of full sun. Similarly, we (J.B. Skillman and K. Winter, unpublished data) found that differences in nocturnal acidification between HL and LL *A. magdalenae*, although statistically significant, were surprisingly small (148 ± 25 and 104 ± 7 mmol H^+ m^{-2} in HL and LL plants, respectively). Finally, Table III suggests that, although the duration of phase III was longer in HL than in LL plants, in most cases plants were CO_2-limited for a substantial portion of the day. Thus, even when HL plants were exposed to a controlled daily irradiance of approximately 12 mol m^{-2} in the high light growth chambers (which is approximately half of the mean daily growth irradiance for these plants; see "Materials and Methods"), the malate pool was insufficient to support phase III photosynthesis for more than a few hours (Fig. 7; Table III). These observations indicate a limited plasticity for increasing the maximum malate pool size in response to growth in high light in *A. magdalenae*. This may in turn restrict the potential for high light acclimation of photosynthesis without simultaneously increasing the risk of photoinhibition.

CONCLUSIONS

Our findings suggest that during phase III of the CAM cycle *A. magdalenae* in the understory is able to use transient increases in light for photosynthesis with greater efficiency than sympatric C_3 species. Relative advantages for sun fleck use in carbon gain should be important for understory populations of *A. magdalenae*, given the combination of a high maximum rate of photosynthesis, a rapid induction response, and a high substrate CO_2 supply. It remains to be seen to what extent this observation also applies to other shade-tolerant CAM plants.

Results from the shadehouse study indicate that in *A. magdalenae* the maximum rate of photosynthetic electron transport appears to vary with the time of day but is unaffected by the growth irradiance, contrasting sharply with that of typical C_3 plants. Despite the limited plasticity in photosynthetic capacity, *A. magdalenae* displays enormous variation in the maximum level of photoprotective energy dissipation, having among the highest reported values of NPQ for high light grown plants.

Even with a high potential for dissipative nonphotochemical quenching and a high rate of photosynthesis (for a shade plant), *A. magdalenae* was chronically photoinhibited under full sun conditions. From the relationship between the photoinhibitory response to a known light dose and the apparent duration of phase III, we developed a hypothesis that may have some bearing on the apparent absence of light acclimation potential in *A. magdalenae*. We speculate that in constitutive CAM plants an increase in the maximum rate of photosynthesis as a response to growth in high light without a proportional increase in the malate supply would predispose these plants to severe chronic photoinhibition.

More generally, this study increases our understanding of the implications of constitutive CAM for leaf carbon gain in low light mesic sites and illustrates how a single physiological trait in a single species (CAM in *A. magdalenae*) might have different functional consequences in different habitats, e.g. efficient use of sun flecks for carbon gain in shaded sites and tolerance of light stress in sun-exposed sites.

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